

What's New in Plant Physiology

Responses of respiration to increasing atmospheric carbon dioxide concentrations

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It has been recently recognized that increases in carbon dioxide concentration such as are anticipated for the earth's atmosphere in the next century often reduce plant respiration. There can be both a short-term reversible effect of unknown cause, and long-term acclimation, which may reflect the synthesis and maintenance of less metabolically expensive materials in plants grown at elevated carbon dioxide concentrations. Because respiration provides energy and carbon intermediates for growth and maintenance, reductions in respiration by increasing carbon dioxide concentrations may have effects on physiology beyond an improvement in plant carbon balance. As atmospheric carbon dioxide concentration increases, reduced respiration could be as important as increased photosynthesis in improving the ability of terrestrial vegetation to act as a sink for carbon, but it could also have other consequences.

Key words – Acclimation, carbon dioxide concentration, global climate change, relative growth rate, respiration.

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Introduction

Respiration provides energy for use in vital cellular processes such as the synthesis of biochemical compounds needed for tissue growth and repair, protein turnover, the maintenance of ion gradients and the transport of various substances. It has been known for many years that very high carbon dioxide concentrations (several thousand $\mu\text{l l}^{-1}$) reduce respiration. These concentrations can be used to prolong the storage life of fruits and vegetables. However, it has only recently been recognized that the increases in carbon dioxide concentration anticipated for the earth's atmosphere in the next century (e.g. up to 700 $\mu\text{l l}^{-1}$) often substantially reduce plant respiration. This effect may have an important impact on the time course of changes in the carbon dioxide concentration in the earth's atmosphere, as well as alter the response of plant growth to increasing carbon dioxide concentrations. There can be both a short-term effect of carbon dioxide concentration on respiration and long-term acclimation.

climation to increased carbon dioxide concentrations can either increase or decrease respiration rates measured under standard conditions.

The rate of respiration generally increases with the rate of growth and with biomass. We would expect that as plant growth rates increase with increasing carbon dioxide concentrations because of the stimulation of photosynthesis, respiration rates would also increase. While this has occasionally been observed, the much more common response is that the respiration rate decreases or remains the same at elevated carbon dioxide concentrations, despite an increase in photosynthesis and growth rate (cf. Bunce and Caulfield 1991). It appears that carbon dioxide concentration can modify the physiological relationship between respiration rate and growth rate.

Abbreviations – RGR, relative growth rate.

Respiration and growth

When plant growth rates change, for example during ontogeny or by altered light regime, it has commonly

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been observed that respiration (dark carbon dioxide efflux) per unit of mass increases linearly with the growth rate per unit of mass, the relative growth rate (RGR), above some minimum value at zero RGR. These observations led to the growth and maintenance model of plant respiration, which formalizes the concept that some respiration is associated with maintaining the existing biomass and some with the synthesis of new tissue. The slope of the linear relationship defines the coefficient of growth respiration, and the respiration rate at zero RGR defines maintenance respiration. There are some difficulties in using relationships between respiration and RGR to separate respiration into its growth and maintenance components. For example, the assumption is made that respiration proceeds at the same rate (at constant temperature) in the light as in darkness. It is also assumed that no significant change in storage materials occurs from day to day, and that the rate of maintenance respiration is independent of RGR. The former assumption has been debated for many years and is difficult to assess experimentally. The latter assumption is known to be violated, with maintenance respiration often increasing with increased RGR. Growth respiration can also be estimated from single values of respiration and RGR coupled with analysis of the composition of the tissue and the respiratory costs associated with its synthesis. Respiratory costs of synthesis are estimated from the energy requirements of the biochemical pathways involved (Penning de Vries et al. 1974). Using single values of respiration and RGR eliminates the need to assume that maintenance respiration is independent of RGR.

When we examine the effect of growth at different carbon dioxide concentrations on respiration rate, we must recognize that differences in RGR would affect the comparison of respiration rates. It is common for the RGR to be higher for plants grown at a higher carbon dioxide concentration, but often higher RGR occurs for only a limited period of time. It cannot be assumed that just because plants grown at a higher carbon dioxide concentration have greater biomass, they currently have a higher RGR. Lack of information on RGR limits the usefulness of many reports of respiration rates for plants growing at different carbon dioxide concentrations. The same problem occurs for rates of respiration of single leaves, because fully expanded leaves may still have substantial RGR.

There may be a simple reason for respiration rates to be lower in plants growing at elevated carbon dioxide concentrations at the same RGR, but whether this explanation actually applies is not established. Plants growing at an elevated carbon dioxide concentration may be constructing and maintaining less energetically expensive biomass. For example, tissue protein and nitrogen contents are often less in plant material produced at elevated carbon dioxide concentrations. Since protein turnover is a substantial component of maintenance respiration, there is often a positive correlation between tissue nitrogen content and maintenance respiration. Also, since proteins

are fairly expensive to synthesize, the coefficient of growth respiration might be less in elevated carbon dioxide concentrations.

However, the only study so far which used chemical analysis of the tissue to directly estimate growth respiration for different carbon dioxide treatments found no significant differences in the respiratory costs of tissue synthesis in spite of differences in tissue nitrogen content in the C_4 species, maize (Loomis and Lafitte 1987). Differences in nitrogen or protein content do not automatically imply differences in construction or maintenance costs, because offsetting changes in the content of carbon, lipids, lignins, etc. may occur. Studies which have used relationships between respiration rate and RGR to separate growth and maintenance respiration have found either a small decrease or no change in the coefficient of growth respiration, but a major decrease in maintenance respiration at elevated carbon dioxide concentrations (Bunce and Caulfield 1991, Wullschlegel and Norby 1992, Wullschlegel et al. 1992). While Wullschlegel et al. (1992) found that the decrease in maintenance respiration at elevated carbon dioxide concentration correlated with lower nitrogen content, Ziska and Bunce (1993) found situations where maintenance respiration was lower at high carbon dioxide concentration even when there was no decrease in protein content.

A major limitation with all of these studies which have attempted to separate respiration into its growth and maintenance components is that the short-term reversibility of the inhibition of respiration by high carbon dioxide concentration was not examined. Because of this, direct effects of carbon dioxide concentration on respiration rate rather than indirect effects based on change in composition cannot be ruled out. In fact, the differences in respiration rates in *Castanea sativa* shoots grown at ambient and elevated carbon dioxide concentrations were completely reversible within minutes (El-Kohen et al. 1991) when rates were expressed on a unit leaf area basis. I have obtained the same result with *Scirpus olneyi* stems and *Quercus prinus* leaves with respiration rates expressed either per unit of area or per unit of mass. Short-term reversibility of the effect of long-term growth at elevated carbon dioxide concentrations on respiration rate argues against an effect caused by changes in composition, unless the rate and nature of materials synthesized can be immediately affected by carbon dioxide concentration. This has not been examined, to my knowledge.

Short-term response and acclimation

An immediate, reversible response of respiration rate to carbon dioxide concentration is common, but variable in magnitude, and not universal. The rate of respiration measured at 350 $\mu\text{l l}^{-1}$ carbon dioxide concentration ranged from 1.01 to 1.54 times that measured at 700 $\mu\text{l l}^{-1}$ in a study of soybean, tomato and amaranth grown at these two carbon dioxide concentrations (Bunce 1990), while factors of greater than 2 were sometimes found in

Castanea sativa shoots (El-Kohen et al. 1991). There is insufficient information to generalize about how much or why the magnitude of the short-term response of respiration rate to carbon dioxide concentration varies with growth or measurement conditions, age or species.

Several possible mechanisms for a short-term response of respiration rate to carbon dioxide concentration can be envisioned, but none has been firmly established. One possibility is that dark fixation of carbon dioxide is stimulated by high carbon dioxide concentrations, and that what is observed is a reduction in the net rate of carbon dioxide efflux and not a real reduction in respiration rate. While a stimulation of dark fixation seems possible, there is evidence that respiration is, in fact, reduced at high carbon dioxide concentrations. For example, oxygen uptake is also reduced by high carbon dioxide concentrations (Gale and Berry 1991, Gifford et al. 1985), and adenosine 5' triphosphate content was reduced after brief exposure to an elevated carbon dioxide concentration (Shaish et al. 1989). There are several reports of inhibition of a variety of respiratory enzymes by very high carbon dioxide concentrations in fruits (cf. Amthor 1991). It is not unreasonable that, in tissue in which carbon dioxide concentrations are normally much less than in fruits, such enzymes might be sensitive to air levels of carbon dioxide; however, data are lacking.

Acclimation of respiration to growth carbon dioxide concentration has not been explicitly examined, however some data can be interpreted to indicate that both positive and negative acclimation can occur. Negative acclimation, a long-term reduction in rate at a constant measurement condition, has been observed in plants which were exposed to higher carbon dioxide concentrations only in the daytime (Baker et al. 1992). Positive acclimation is indicated by cases in which the immediate decrease in respiration at an elevated measurement concentration greatly exceeded any long-term reduction in rate (Bunce 1990). Clearly more studies are needed which examine both the short-term and the long-term responses of respiration to carbon dioxide concentration and their relationship to tissue composition and to RGR.

Implications

If reduced carbon dioxide efflux in the dark reflects a reduction in the rate of energy supply for vital plant functions, it may have consequences beyond simple conservation of carbon. The reduction in stomatal conductance to water vapor often observed in leaves at elevated carbon dioxide concentrations may be one example. Experiments by Shaish et al. (1989) suggest that reduced stomatal conductance at elevated carbon dioxide may result from an inhibition of respiration by guard cells and a diminished ability to maintain the ion gradients responsible for the turgor-pressure-induced opening of these cells in the light. There is also evidence suggesting that reduced respiration may sometimes be involved in the reduction in photosynthetic capacity which is com-

monly observed in plants grown at elevated carbon dioxide concentrations. Exposure of soybean leaves to an elevated carbon dioxide concentration for only one night resulted in the same reduced photosynthetic capacity as that of leaves exposed to the higher carbon dioxide concentration throughout development (Bunce 1992a). Gale (1982) reported that reduced respiration rate caused either by increased carbon dioxide concentration or by reduced oxygen concentration in the dark reduced photosynthetic capacity the following day in *Xanthium strumarium* leaves.

A reduction in dark carbon dioxide efflux rate by high carbon dioxide concentrations obviously results in a more positive plant carbon balance. A benefit to carbon balance was clearly shown in studies in which the dry matter accumulation rate of alfalfa plants was increased by exposing plants to increased carbon dioxide concentration only during the dark period (Reuveni and Gale 1985).

A reduction in respiration by plants as atmospheric carbon dioxide concentration increases would increase their ability to act as a sink for carbon. In mature ecosystems, photosynthesis is approximately balanced by respiration. Therefore a decrease in respiration as atmospheric carbon dioxide concentrations increase could be just as important as an increase in photosynthesis to the ability of ecosystems to sequester carbon. In forest ecosystems, which have the largest biomass carbon pool, ecosystem respiration is dominated by autotrophic respiration. Although effects of carbon dioxide concentration on respiration have not yet been examined in large trees, reductions have been found in leaves of tree saplings (Wullschleger and Norby 1992, Wullschleger et al. 1992) and in whole tree seedlings (Bunce 1992b) with a doubling of the current carbon dioxide concentration. Ecosystem respiration was reduced per unit of ground area in alfalfa plots (Bunce and Caulfield 1991) and in the tundra (Hilbert et al. 1987) during growth at increased carbon dioxide concentrations, suggesting that reduced respiration caused by increased carbon dioxide concentrations may indeed promote ecosystem carbon storage, at least in the short-term. The long-term storage of carbon in terrestrial ecosystems is influenced by many factors in addition to autotrophic respiration and photosynthesis, especially the temperature, moisture and nutrient regimes, and the function of decomposers. In this regard, it is interesting that the respiration rate of some soil microbes responsible for decomposition may also be reduced by increasing carbon dioxide concentrations (Koizumi et al. 1991).

While changes in ecosystem carbon storage are of obvious relevance to the current environmental situation, one also wonders if it is a coincidence that during the Mississippian and Pennsylvanian Periods, when major coal deposits were formed, the atmospheric carbon dioxide concentration was several times higher than the current concentration.

Clearly we need to know the mechanisms by which

carbon dioxide concentration affects rates of respiration before we can fully assess the implications of this response for plant carbon balance and growth and for ecosystem carbon storage in the face of increasing atmospheric carbon dioxide concentrations.

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